The Natural History of *Haliclona ecbasis* de Laubenfels, a Siliceous Sponge of California[1]

PAUL E. FELL[2]

LITTLE INFORMATION concerning the haliclonids of the Pacific Coast of the United States is presently available. De Laubenfels (1933) described briefly several haliclonids of California, but gave no account of their reproduction. During a study of oogenesis and embryonic development in *Haliclona ecbasis* de Laubenfels (Fell, 1969), information relating to the habitat, morphology, and breeding seasons of this sponge was also accumulated. This material is the subject of the present paper.

GENERAL DESCRIPTION

All of the specimens of *Haliclona ecbasis* included in this study were obtained from the Berkeley Yacht Harbor on San Francisco Bay. However, this sponge has also been collected at the St. Francis Yacht Harbor in San Francisco. In addition, a few specimens of what appeared to be *H. ecbasis* were seen at other yacht harbors on San Francisco Bay (at Sausalito and at Redwood City), and others were collected in rocky intertidal regions near Carmel, California.

In the yacht harbors, *H. ecbasis* is found attached to the floats but never to the pilings. Most usually this sponge forms thick encrustations on the masses of mussels which cling to the floats; however, it also encrusts styrofoam, wood, and other surfaces. While specimens of *H. ecbasis* are frequently attached along the sides of the floats, they appear to be more abundant on the shaded undersurfaces.

H. ecbasis varies in color from a dull brown to a rich golden brown. However, regions of the sponge exposed to bright sunlight are frequently pinkish lavender. This lavender color is not restricted to the surface of the sponge, but rather it may extend throughout the upper half of the endosome in horizontal branches.

This sponge has a soft, compressible consistency, and, like many other sponges, it has a variety of forms (Fig. 1). Frequently it occurs as thick masses with stout, closely set oscular tubes; but it also occurs in the form of irregular tubes which branch and reunite, of club-shaped lobes with oscular openings at various points along their length, or of a thin sheet with low oscular tubes scattered over the surface. The oscular openings range in diameter from about 1 to 3 mm.

The principal skeleton consists of monaxonid spicules held together in a lattice by spongin. In the lattice, parallel columns of from one to six spicules in cross section, situated perpendicular to the surface of the sponge, are joined by horizontally placed individual spicules and chains of from two to four spicules fastened end to end (Fig. 2). Some short horizontal tracts of two or more spicules in cross section are also observed. Usually only the ends of the spicules appear to be enclosed in spongin. In addition to the lattice, tracts of unjoined spicules running parallel to the surface of the sponge and isolated spicules are found.

Most of the spicules are oxeas, but scattered styles also occur. The oxeas are typically about 120 to 130 μ long and about 7 μ wide. The average lengths of the oxeas for four specimens, collected at different times, ranged from 119 to 133 μ, while the absolute range in length was from 84 to 145 μ (Table 1). The average widths of the oxeas in these specimens ranged from 5.5 to 7.4 μ, and the absolute range was from 1.8 to 9.0 μ. The styles tended to be somewhat shorter and stouter than the average size of the oxeas in any specimen.

For histological studies, specimens of *H. ecbasis,* fixed in Bouin's solution in artificial sea water, were embedded in paraffin and sectioned serially at 8 μ. The mounted, deparaf-

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[2] Present address: Department of Zoology, Connecticut College, New London, Connecticut 06320.

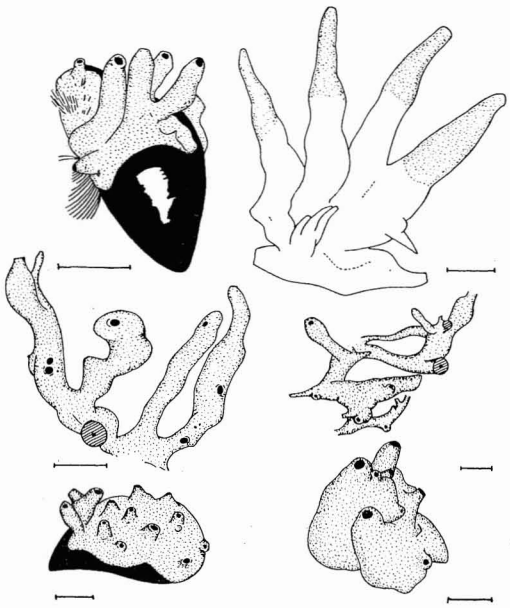

FIG. 1. Different growth forms of *Haliclona ecbasis* (drawn from life) collected at the Berkeley Yacht Harbor. The lower part (unstippled) of the specimen on the upper right consisted of skeleton impregnated with debris. The scale line in each case is approximately 1 cm.

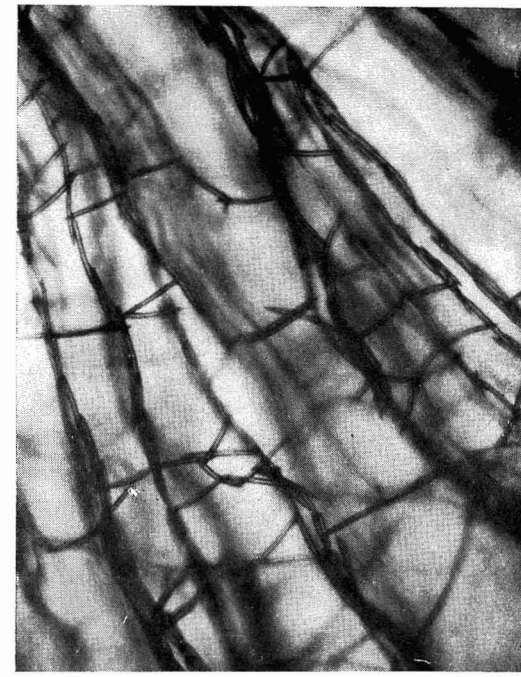

FIG. 2. A portion of an intact skeleton of *Haliclona ecbasis* cleaned of cellular components by soaking the specimen in a detergent solution. Magnification ca. 70×.

finized sections were then stained with Mayer's hematoxylin and eosin.

The dermal membrane is thin and seems to consist of two layers of pinacocytes between which other cells are frequently situated. It does not contain spicules. The inner layer of pinacocytes is a part of the lining of the prominent subdermal cavities. The dermal membrane is supported by the vertical columns of spicules and extensions of the endosome through which the columns course.

Cells with strongly eosinophilic cytoplasm are associated with, and largely restricted to, the dermal and subdermal regions. Such cells are generally abundant near the ends of the skeletal columns, but they are also seen in the dermal membrane and surrounding the subdermal cavities. These cells are approximately 8.5 μ in diameter and have a granular nucleus about 2 to 3 μ in diameter. They occur either singly or in compact clusters.

The endosome, through which the canal systems ramify, consists of flagellated chambers, tracts of amoebocytes, scattered mesenchymal cells, and frequently reproductive elements. The flagellated chambers are spherical to ellipsoidal and range in size from about 13 × 20 μ to approximately 30 × 40 μ. The bodies of the choanocytes are about 3 μ in diameter; and the nuclei, which stain deeply and lack obvious nucleoli, are approximately 1.5 μ in diameter. Usually the nuclei are somewhat flattened against the bases of the cells. Many of the flagellated chambers contain one or more irregularly shaped cells within their lumina. These cells have a pale nucleus about 2.5 to 3 μ in diameter with a small nucleolus.

The tracts of amoebocytes course through the endosome in various directions and may partially surround some of the canals. Such tracts range in diameter from about 15 μ to approximately 66 μ. The amoebocytes of the tracts vary in size, and frequently included among them are cells which are indistinguishable from nurse cells (Fell, 1969). Typical spicules, together with some very fine spicules, are observed in many of the tracts.

TABLE 1

SPICULE DIMENSIONS (IN MICRONS) OF *Haliclona ecbasis*[1]

SPECIMEN	OXEAS		STYLES	
	LENGTH	WIDTH	LENGTH	WIDTH
10-8-64 L	118–**133**–142 [± 5.2]	4.2–**7.4**–9.0 [±1.01]	115 and 123 (2)	6.0 and 7.8 (2)
8-9-65 C	100–**130**–145 [±11.0]	3.0–**5.5**–7.2 [±1.23]	–	–
8-23-65 E	86–**124**–139 [±11.7]	3.0–**7.2**–9.0 [±1.68]	103–**111**–122 (4)	6.6–**7.4**–8.4 (4)
9-22-65 N	84–**119**–130 [± 9.6]	1.8–**7.1**–9.0 [±1.63]	105 (1)	7.8 (1)
All specimens	84–**127**–145 [±11.2]	1.8–**6.8**–9.0 [±1.59]	103–**114**–123	6.0–**7.3**–8.4

[1] The ranges, means (in boldface), and standard deviations (in brackets) are given for the oxeas; and the ranges and means are given for the styles. The figures for the oxeas are based on 50 spicules per specimen. The number of styles measured in each case is given in parentheses.

In *H. ecbasis,* as in most other sponges, there are no gonads, and the gametes occur scattered about in the mesenchyme. Furthermore, since this sponge is viviparous, oocytes and embryos are usually intermingled. The oocytes range in average diameter (av. of length + width + thickness) from approximately 8.5 μ up to about 140 μ, and the embryos are the same size as the largest oocytes. A total of 86 embryos from five specimens ranged in average diameter from 129 to 163 μ; the average values for the five specimens were 138 μ, 139 μ, 139 μ, 150 μ, and 154 μ. The oocytes and embryos have been described in detail elsewhere (Fell, 1969).

Spermatogenesis occurs within masses of cells surrounded by a single layer of flattened follicle cells. These masses, which are distributed throughout the endosome, vary in size and appear to be composed of from one to several clusters of cells. However, since it is frequently difficult to distinguish the boundaries of the follicles, adjacent follicles may be mistaken for a single large follicle. All of the cells of a cluster are in the same stage of differentiation, but all of the clusters in a follicle may not be. The cells evidently undergo a series of divisions in the course of which they become progressively smaller, and finally they differentiate into spermatozoa. No study of the divisions has been made, but it seems likely that they include two reduction divisions. The spermatozoa have a spherical head about 0.6 μ in diameter and a flagellum roughly 10 μ in length.

Three gemmules were observed in histological sections of a single specimen of *H. ecbasis.* The gemmules were situated in the basal endosome in which numerous diatoms also were seen. Each gemmule was enclosed within a capsule of spongin, and spicules were embedded in the capsule on one side. The spicules (oxeas) were about 110 μ long and 6 μ wide in two of the gemmules (the range for 10 spicules from each gemmule was 103 to 118 μ × 6 to 7.2 μ) and were apparently shorter and much narrower (about 3.8 μ) in the third. The spongin layer in regions of the capsule devoid of spicules was about 3 to 12 μ thick. Two of the gemmules were found to have an average diameter (av. of length + width + thickness) of 312 μ and 259 μ, respectively.

The gemmules were of different types suggestive of developmental stages. In what appeared to be the earliest stage represented, the central region was occupied by cells approximately 8.5 μ in diameter, with finely granular cytoplasm. Some granular cells and many smaller cells that stained strongly with hematoxylin were situated peripherally beneath the capsule, and many of them were oriented perpendicular to it. In what appeared to be the latest stage there were no small, darkly staining cells, but only cells of about 15 μ diameter with coarsely granular cytoplasm.

BREEDING SEASONS

In order to obtain information on the breeding seasons of *Haliclona ecbasis,* nearly 100 specimens, collected over a period extending from 1964 through 1966, were examined. The specimens were fixed in Bouin's solution in artificial sea water, and each one was dissected and examined under a dissecting microscope for the presence of embryos. Then small pieces of the specimens were processed for histological examination. In most cases, 30 spaced, serial

sections were scanned at a magnification of approximately 1,000× to determine the presence or absence of gametes.

From the evidence presently available it appears that there are two breeding seasons, or at least two reproductive peaks, one in the spring and another in the fall (Table 2). During the spring and fall of 1964 and the late summer and fall of 1965, numerous gametes and embryos were found in many sponges. Also in the spring and in the fall of 1966 a few specimens with numerous reproductive elements were observed. However, interpretation is complicated by the fact that *H. ecbasis* was absent (or extremely scarce) at the Berkeley Yacht Harbor during the summer of 1964 and the first few months of 1965, and also by the fact that only few observations were made in 1966.

Although some reproductive sponges can usually be found whenever the species is abundant, observations made during the summer and fall of 1965 suggest that both the frequency of specimens containing embryos and/or gametes and the number of embryos and/or gametes contained in the specimens varies with the season (Table 3). For example, during the 2-month period from May 17 to July 13, 8 of 12 specimens collected contained gametes; and only 1 (8 percent) possessed large numbers of them. Furthermore, only 1 of 6 specimens with oocytes possessed large ones, and none of the specimens contained embryos. By contrast, during the 4-month period from July 19 to November 18, 40 of 42 specimens collected (95 percent) were reproductive and 35 (83 percent) contained large numbers of gametes and/or embryos. This reproductive peak was apparently followed by a gradual decline. Although 90 percent of the specimens collected during the period from November 30 to January 7 contained embryos and/or gametes, only 40 percent possessed them in large numbers. Furthermore, 15 specimens collected during the winter of 1966 (4 in addition to the 2 recorded in Table 3 on January 7, 4 on January 21, 4 on February 3, and 3 on March 3) were examined under a dissecting microscope; and only 2 of the specimens (from January 7) contained large oocytes and/or embryos. Since no histological examination was made of these specimens, it is not known whether any of them contained small oocytes or sperm (hence the question marks in Table 2).

Water temperature has been shown to be a factor regulating the breeding season in several sponges (see, for example, Orton, 1920; Storr, 1964; and Simpson, 1968). In *H. ecbasis* the reproductive peaks appear to occur when the water temperature is rising or high (see Table 2), but it is not known whether this temperature has any direct influence on reproduction.

Of the 64 specimens recorded in Table 3, 16 were apparently male, containing only sperm,

TABLE 2

OCCURRENCE OF REPRODUCTIVE SPECIMENS OF *Haliclona ecbasis* AND MONTHLY MEANS IN WATER TEMPERATURE AT THE BERKELEY YACHT HARBOR, FROM JANUARY 1964 TO OCTOBER 1966

	1964		1965		1966	
MONTH	GAMETES AND/OR EMBRYOS	TEMPERATURE (°C)	GAMETES AND/OR EMBRYOS	TEMPERATURE (°C)	GAMETES AND/OR EMBRYOS	TEMPERATURE (°C)
January	+	–	*	–	+	9.3
February			*	–	?	10.5
March	+	–	*	–	?	–
April	+	–	*	–		
May	+	–	–	–	+	17.0
June	*	16.0	+	17.5		
July	*	–	+	17.5		
August	*	20.0	+	18.5		
September	+	17.5	+	17.5	+	–
October	+	17.5	+	17.0	+	–
November	+	12.0	+	13.5		
December			+	9.5		

* No or few specimens were found.

TABLE 3

ANALYSIS OF THE 1965–1966 REPRODUCTIVE SEASON OF *Haliclona ecbasis* AT THE BERKELEY YACHT HARBOR

DATE	NUMBER OF SPECIMENS EXAMINED	GAMETES AND EMBRYOS IN THE SPECIMENS			
		NONE	FEW	MANY	TYPES[1]
May 17	1	1			
June 17	4	2	1	1	sO, O
25	2		2		S, sO
28	3		3		3 sO
July 6	1	1			
13	1		1		S
19	4	1		3	S, 2 OE
24	2			2	S, SsO
Aug. 9	3		1	2	S, sOE, OE
23	3		1	2	S, 2 OE
Sept. 7	2			2	S, OE
8	6			6	SsO, sOE, 4 OE
13	3			3	3 OE
22	11		2	9	2 S, SOE, SEG, sO, sOE, 5 OE
Oct. 5	3	1	1	1	S, OE
28	3			3	S, SOE, sO
Nov. 18	2			2	2 S
30	4		3	1	3 S, OE
Dec. 17	4	1	1	2	sO, sOE, O
Jan. 7	2		1	1	2 sO

[1] S = Sperm, sO = small oocytes, O = all stages of oocytes, E = embryos, G = gemmules.

and 35 were apparently female, containing oocytes and/or embryos, or approximately twice as many females as males. In addition, during the peak of the reproductive season 5 specimens containing sperm and oocytes (and/or embryos) were found, in 3 of which there were large numbers of both types of gametes. It is not altogether clear from these data whether *H. ecbasis* is truly dioecious or proterogynous. If it is dioecious, the specimens containing both types of gametes would be considered abnormal individuals and it is unlikely that as many as 8 percent of a population would show such abnormality. If it is a proterogynous species, these specimens presumably would be in a stage transitional between producing one kind of gamete and the other.

In two specimens of *H. ecbasis* (collected on September 8, 1965) some of the smaller oocytes possessed two nuclei. Such oocytes have also been observed in other siliceous sponges (Leveaux, 1941; Lévi, 1956), where they have been considered to be abortive. However, since fertilization has not been observed in *H. ecbasis*, the possibility that the two nuclei represent male and female pronuclei can not be excluded (Tuzet, 1964).

Finally, several gemmules, in addition to an embryo and sperm, were found in a single specimen collected on September 22, 1965.

TAXONOMIC DISCUSSION

Much emphasis has been placed on skeletal characteristics in the classification of sponges. However, as has been emphasized by Hartman (1958), identification of haliclonids on the basis of such characteristics alone is difficult because these sponges possess only one type of spicule and there is wide intraspecific variation in skeletal structure. Identification is further complicated by the fact that color, form, and other characteristics may also be highly variable. Consequently, fully adequate descriptions must be based on the examination of relatively large numbers of specimens and must include as many characteristics as possible.

The sponge described in this paper is tenta-

tively considered to be *Haliclona ecbasis* (de Laubenfels, 1933). However, in general form, spicule dimensions, and the production of gemmules (although apparently rare), it resembles *H. loosanoffi* from the northeastern coast of the United States (Hartman, 1958). A firm decision on taxonomic status must await more extensive data both on the sponge in question and on other haliclonids which have been described. Of particular importance will be cytological and developmental information.

SUMMARY

A general description is given of *Haliclona ecbasis* de Laubenfels from the Berkeley Yacht Harbor on San Francisco Bay. Studies on the reproduction of this sponge are also reported. There appear to be two reproductive peaks, one in the spring and another in the fall, although some specimens with reproductive elements may be found at other times of the year. Most of the specimens contain only one type of gamete, but some contain both. Female specimens appear to be about twice as abundant as male specimens.

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